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A Study of the
Cause of "Buttons"
in the
J. H. Hale Peach

By M. J. DORSEY

UNIVERSITY OF ILLINOIS
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A Study of the Cause of "Buttons" in the J. H. Hale Peach

M. J. DORSEY, Chief in Pomology

NO PEACH was ever received with so much enthusiasm from growers and pomologists as the J. H. Hale variety when it was introduced by the Wm. P. Stark Nursery Company, of Stark City, Missouri, in 1912 (Hale^{12*}). As it was more generally planted, however, two serious defects became apparent. In the first place, it was reported (Conners^{3*}) to bear aborted anthers; and therefore to be pollen-sterile. In the second place growers observed that a variable proportion of the crop in some seasons did not reach full size^a but remained upon the tree to ripen somewhat later than the normal fruit. This contrast in size of fruit is shown in Fig. 1.

These defects were indeed serious in a variety which seemed so promising in the initial tests. Expressions of enthusiasm in the early writings, such as "the million dollar peach" and "Elberta is doomed," soon gave way to adverse criticism when it became apparent that, because of low yield, this variety was not so profitable as it had promised even tho it did command a high price in the market. It is only fair to state, however, in support of the high estimate placed upon its merits after the first tests, that Culpepper and Caldwell^{4*} found it to rank above all other commercial freestones grown in the East in retaining its firmness after picking and in holding together in the canning process.

The production of aborted anthers and buttons by this variety would not be so serious were it not for the fact that it also falls short of some of the other varieties in hardiness of fruit bud and in vigor of growth. Because of these shortcomings, J. H. Hale has not been set so extensively in commercial orchards in the last decade as previously. Nevertheless the unusually attractive appearance and carrying quality of the fruit still make it a favorite in the "fancy" trade, especially when distance shipments are involved.

^aThe small fruits borne by this variety have become known by different names, such as "buttons," "runts," "nubbins," or simply the "little fellows." The term "button" first used in 1922 in New Jersey (Blake *et al**) will be used in this connection because its use with this meaning has become well established among peach growers.

*These and similar numbers throuth the text refer to literature citations, page 43.

Recognizing that there is considerable interest in J. H. Hale among peach breeders, and that it is still an important variety in some places, it seemed advisable to determine, if possible, the cause of the retarded growth which terminates in buttons. This information would, of course, serve also as a basis for understanding this problem in whatever variety of the peach it may occur.

EXTENT OF BUTTON PRODUCTION

Button production is quite variable from year to year. While in extreme instances as many as 90 percent of the peaches which remain upon the tree after the June drop may develop into buttons, generally the proportion is not so large. In some orchards the button problem seems to be much less serious over a period of years than in others. Trees in good vigor may not produce buttons one season but in the next season may bear buttons in abundance. Old trees seem to produce more buttons the year following a heavy crop, but this relationship is not constant. Sometimes only a few trees in an orchard will bear buttons. In one instance in 1931 a single limb on a fourteen-year-old J. H. Hale tree bore buttons in clusters, while the remainder of the tree was practically free from them. The seriousness of button production in this variety will be seen from the following records.

In a J. H. Hale block in the Bates orchard near Centralia, which was under observation in 1929, button production was quite general. In a careful count of the crop on ten typical trees the first of August, the following condition was found: The number of buttons ranged from 79 to 356 per tree and the number of normal fruits from 76 to 404 per tree. The total number of buttons on these ten trees was 1,784; the number of normal fruits, 2,012. The tree which bore the largest number of buttons, 356, produced only 115 normal fruits. In this same orchard the years 1927, 1928, 1929, 1933, and 1935 were "button years," while in 1926 and 1931 practically no buttons were produced.

An unusual situation developed in another orchard in southern Illinois in the spring of 1936. Fruit-bud survival after the winter temperatures was about 8 percent—enough for a crop if all were to set and mature. Sometimes good crops are produced under just such conditions. But in this orchard freezing temperatures occurred during bloom and only a few of the fruits developed normally altho there was an abundance of buttons. This instance would seem to bear out the suggestion that buttons result from low-temperature injury.



FIG. 1.—A NORMAL J. H. HALE PEACH AND TWO "BUTTONS"
JUST BEFORE HARVEST
(Natural size)

Still another opportunity arose in the spring of 1938 to observe button production in an orchard near Flora, Illinois. J. H. Hale had been planted alternately in 4-row blocks with Elberta. The weather was unfavorable for bee flight during bloom, altho there was an abundance of bloom for a crop. At first it seemed that the set was going to be heavy, owing to a very light first drop, but as the season advanced the second drop was excessive, leaving only 300 to 500 fruits per tree. The June drop proved to be light on both J. H. Hale and on the adjacent trees of Elberta. On June 24, after all three of the drops were over, the number of normal peaches on fifteen J. H. Hale trees was as follows: 16, 9, 26, 20, 6, 18, 17, 18, 33, 14, 6, 33, 7, 20 and 22. The number of buttons on these same trees was estimated to vary between 150 and 500. These trees were seven years old and capable of bearing a full crop of four or five bushels each. This was the most extreme case of button production observed during this study.

The production of buttons by J. H. Hale is also serious in other sections of the country. Conners^{3*} says: "In some orchards [in New Jersey] this variety will produce a full crop of large, fine peaches, while in an orchard only a short distance away the crop will be practically all buttons." From the Grand Junction District of Colorado, Mr. Silman Smith writes: "The trees bore very nicely as four-year-olds; but as five-year-olds, last year, most of the crop consisted of buttons."^a Other records of a similar nature might be given, but these will suffice to illustrate the situation with the variety elsewhere.

In other varieties button production is not so serious, altho it has been noted in Globe and Crosby (Stewart and Eustace^{22*}), St. John, Fox, Elberta, Foster (Conners^{3*}), Bilmeyer, Bridgon, Early Crawford and Richmond (Palmer^{19*}). The writer observed an instance in 1896 in northern Muskingum county, Ohio (similar to that of Heister below), in which the entire crop of Early Crawford and a local yellow freestone known as Crabtree were buttons. Buttons have also been found recently in some of the newer varieties, such as Halberta and Fertile Hale.

It is apparent, then, that this condition may occur in other varieties although the experience of growers shows that the problem is centered for the most part in the variety J. H. Hale. The economic importance of the button situation, therefore, lies in the fact that a full crop in prospect may be reduced to an unprofitable partial crop as in the instance reported by Heister.^{15*}

^aPersonal letter, May 19, 1930.

OTHER OBSERVATIONS ON CAUSE OF BUTTONS

A survey of the literature shows that buttons have been ascribed to a number of causes. Heister^{15*} made the following record of a personal experience:

"In 1896 about 3,000 of my trees bore a crop of little peaches . . . I cut a great many of them at different times but not a single one had a kernel in the pit . . . I, at the time, decided that owing to some unfavorable climatic condition, the blossoms were not properly fertilized and as there was no seed to ripen, there was no growth to the peach."

The varieties in the Heister orchard were not given, but it is stated that these same trees bore an abundant crop of perfect peaches the next year. Stewart and Eustace^{22*} and Palmer^{19*} also think buttons are a result of "imperfect fertilization."

Connors^{3*} says that these buttons behave as if fertilized, as unfertilized blossoms drop as soon as the petals fall. He writes:

"If pollination has been accomplished, complete fertilization has not taken place. This may be due to the pollen tube being slow in growth so that the tube nucleus enters the ovum at a period too late for fusion. The development of buttons would then be an expression of vegetative vigor."

In a personal letter to the writer (October 10, 1936) Blake says that buttons are "always present following a season when there is cold injury to the flowers and twigs." He states further that buttons are "brought about by the effect of low temperatures upon the stem of the fruit or near its attachment which disturbs the normal movement of nutrients." Something of the same idea is set forth by Harrold,^{13*} in a discussion of drops, when he suggests that "in the course of abortion, development stops first in the region of the chalaza and extends from there to other parts of the seed and fruit.

The writer in 1928 (Dorsey^{9*}) stated that "the causes leading up to the formation of buttons appear to be centered about the early stages of development of the young fruit."

It will be seen from these quotations that both weather and pollination have been suspected of having a bearing upon the production of buttons. Either of these would place the cause of buttons "at the early stages of development." The exact way in which cold injury to the "flowers and twigs" may cause buttons is not clear, but evidence of this relationship needs critical study. It is possible, also, that the disorder in the region of the chalaza, which Harrold suggests may "disorganize the vascular system," is in reality a consequence of a deeper-seated factor. Further consideration will be given to these ideas in the general discussion, pages 28 to 40.

MATERIALS AND METHODS

The first material for this study was collected in 1926 from J. H. Hale trees which were known to be true to name. Since then fruit production in this variety has been studied in a number of orchards in this state and also in the Grand Junction area in Colorado and in the Wenatchee Valley, Washington. The collections of flowers or immature fruits, however, were made primarily from trees in the orchard of D. I. Bates and Son, near Centralia, Illinois. Rawlins fixing fluid was used exclusively in this work and proved very satisfactory.

Fortunately the collections in the Bates orchard included the seasons of 1929 and 1931—two years with the greatest contrast in button production in this orchard and in the state in general. A parallel series of pistils was collected in 1933 for comparison from Elberta trees growing on the University farm near Olney.

The usual cytological technic was followed in embedding and sectioning. Heidenhain's iron alum hematoxylin was used, for the most part, in staining, altho good results were obtained with other stains.

OVULE DEVELOPMENT IN RELATION TO BUTTON FORMATION

This section is devoted to a critical examination of ovules at various growth stages between full bloom and the collapse of the seed about the beginning of the third growth period. This approach to the problem was decided upon because it is impossible to tell which fruits will develop into buttons until after the June drop. Even tho this is true, however, it seemed necessary to study the early stages of development in order to determine whether or not there might be conditions present even then which could be related to button production. Admittedly there is some uncertainty in this procedure, but of course it is impossible to study the internal condition of a pistil and at the same time leave it intact on the tree to complete its normal growth.

The materials on this phase of the problem will be presented in two main parts: (1) the development of the ovule in buttons during the period of the three drops; and (2) the condition found in the seed after the drops are over, when buttons can first be selected with certainty.

Ovule Development During the Drops

Development at Bloom.—Sections of the early pistil stages of J. H. Hale show that the growing point of the ovule in the latitude of southern Illinois is present as early as the middle of March. The

megaspore mother cell, however, is not found until 10 to 12 days before bloom. The growth of the ovule as a whole is relatively rapid after the megaspore appears, and up to full bloom the embryo sac, nucellus, and seed coats undergo the characteristic development of the rosaceous plants, as outlined by Péchoutre.^{20*}

The divisions of the embryo-sac nuclei seem to take place somewhat later in J. H. Hale than in Carman, as reported by Harrold,^{13*} but this point is difficult to check accurately on account of the variation found in the rate or time of development in different pistils. Thus in one series of apparently normal flowers of J. H. Hale collected in 1929 at full bloom the following condition was found in the most advanced ovule of each of the 24 pistils sectioned for examination: in 1 ovule a megaspore had not developed, in 4 a megaspore was present, and in 4 a megaspore was present but degenerating. In the ovules of this lot in which the condition in the embryo sac seemed normal, there was a single nucleus in one sac, two nuclei in 3 sacs, three nuclei in 3 sacs, four in 5 sacs, while only 3 sacs had the full nuclear content of eight (Table 1, line 1).

The condition just described was typical of the other series in J. H. Hale, and of Elberta as well, which were examined at full bloom. In some instances apparently normal embryo sacs did not have eight nuclei as late as one week after bloom. It is quite probable that fertilization would not take place in these sacs if it had already occurred in the more advanced pistils.

Because of so much variation in the nuclear content of the embryo sac at the early stages it does not seem possible to definitely relate a given condition at this time to button formation. It would seem safe to state, however, in view of the three drops which are next described, that the normal fruits would come from those pistils in which the growth and functioning of all of the nuclei in the embryo sac had proceeded normally.

Sixteen Days After Bloom.—At this time in 1929 the young fruits of J. H. Hale in the Bates orchard averaged about $\frac{3}{16}$ inch in diameter and the first drop was nearly over. Slight size differences between the pistils were apparent, but the weaker or aborted ones had already been eliminated by the first drop. Not a single case in which either the zygote or endosperm nuclei had divided was found in 18 pistils sectioned (Fig. 2, *a-d*). In view of the variation noted in the embryo-sac nuclei at bloom, some variation in the nuclear content might still be expected even tho some pistils had been eliminated. Thus, in this sample of 25 pistils there were 4 sacs with no nuclei, 11 with one,

4 with two, 3 with three, 2 with four, while only one sac as late as this had the full nuclear content of eight (Table 1, line 2). This one was probably a late flower. Division had not as yet taken place in the fusion nucleus in any of the pistils of this collection. The presence of a single nucleus in 11 sacs is an interesting feature of this collection. This cell was always in the position in the sac of the female gamete, so it is improbable in these cases that a fusion nucleus was formed. In the absence of fusion, the two nuclei which are destined to form the fusion nucleus by their union are apparently absorbed in much the same manner as the synergids and antipodals.

It will be seen from Table 2 that at the 16-day period the first drop was normally under way. The abscission of those pistils with a single nucleus in the embryo sac in the second drop may be assumed if this

TABLE 2.—COMPARISON OF GROWTH STATUS OF THE DIFFERENT PISTIL OR FRUIT TYPES FOUND IN THE PEACH

Fruit type or growth stage	Size reached before falling	Limit of persistence	Stone length	Seed length	Time of browning of seed coats
First drop of aborted pistils	Full bloom	About 3 weeks
Second drop of nonpollinated pistils as in Elberta	$\frac{1}{2}$ - $\frac{5}{8}$ "	30 to 50 days after bloom	$\frac{1}{8}$ - $\frac{3}{16}$ "	20 to 30 days after bloom
June drop in Elberta and J. H. Hale	$\frac{3}{4}$ - $1\frac{1}{4}$ "	40 to 60 days after bloom	Undergoes partial development	$\frac{1}{4}$ - $\frac{3}{8}$ "	Fruits usually fall before seed coats turn brown
J. H. Hale buttons	$1\frac{1}{4}$ - $2\frac{1}{4}$ "	Until after harvest, 110 to 120 days	1- $1\frac{1}{4}$ "	$\frac{1}{4}$ - $\frac{5}{16}$ "	50 to 80 days after bloom
Buttons with killed seeds	$1\frac{1}{4}$ - $2\frac{1}{4}$ "	Until after harvest, 110 to 120 days	1- $1\frac{1}{4}$ "	$\frac{1}{4}$ - $\frac{5}{16}$ "	Soon after being frozen
Elberta with killed seeds	Full size	Harvest time	Nearly full size	$\frac{1}{4}$ " or so	Soon after being frozen
Normal J. H. Hale fruit	Full size $2\frac{1}{4}$ - $3\frac{1}{2}$ "	Until harvest, 110 to 120 days after bloom	$1\frac{1}{2}$ - $1\frac{3}{4}$ "	$\frac{3}{4}$ - $\frac{7}{8}$ "	Second growth period

type is not found in later collections. If these pistils are disposed of in this way, then a single nucleus in the embryo sac as early as this is of no significance in connection with the buttons. Since 1929 was such a pronounced "button year," it will be interesting to compare the nuclear content of the embryo sac of these pistils with those collected in 1931 at the same relative growth stage, when there were practically

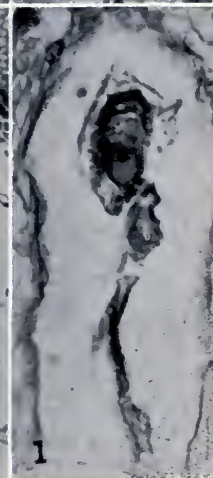
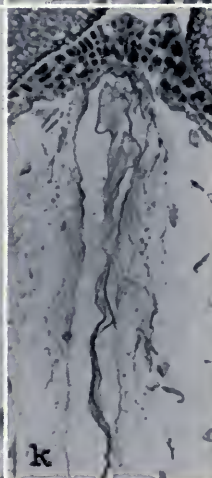
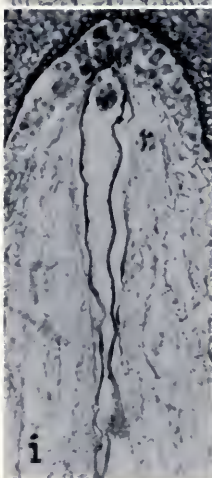
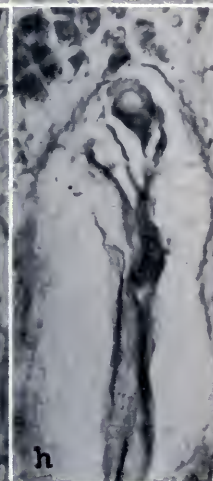
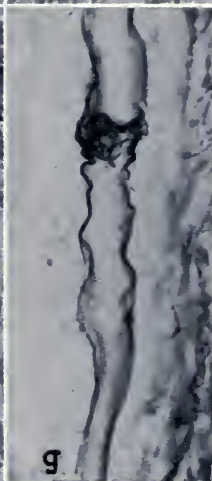
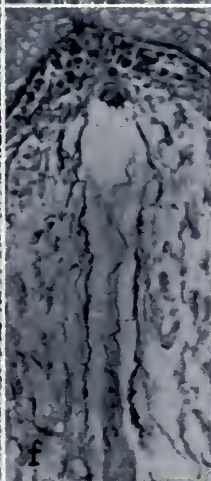
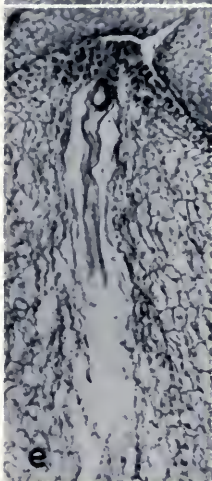
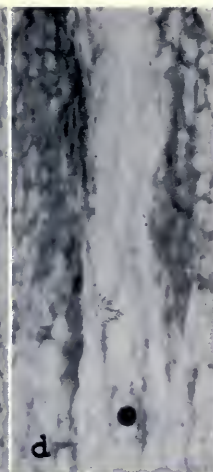
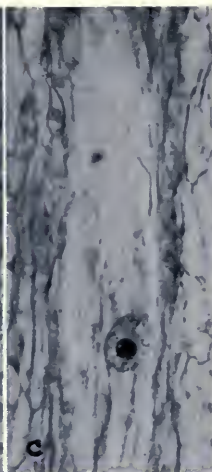
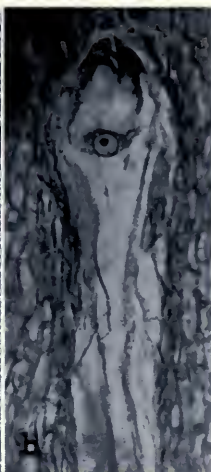


FIG. 2.—CONDITIONS IN EMBRYO SAC AT EARLY STAGES

- a*—An embryo sac 15 days after bloom with only two nuclei—presumably the zygote and the endosperm nucleus.
- b*—A higher magnification of a zygote 15 days after full bloom, showing distended wall and distal position of nucleus in zygote in relation to the micropyle.
- c, d*—Undivided endosperm nuclei 15 days after bloom.
- e, f*—Retarded development in embryo-sac structures three weeks after bloom.
- g, h*—Appearance of undivided endosperm nucleus three weeks after bloom.
 - i*—An embryo 23 days after bloom. Note endosperm nuclei.
 - j*—An endosperm mass in a sac in which there was a zygote remnant, 23 days after bloom.
 - k*—An embryo sac in which the nuclei had been absorbed or completely disintegrated.
 - l*—An undivided zygote nucleus 23 days after bloom. Only a deeply stained remnant was in the position of the endosperm nucleus.

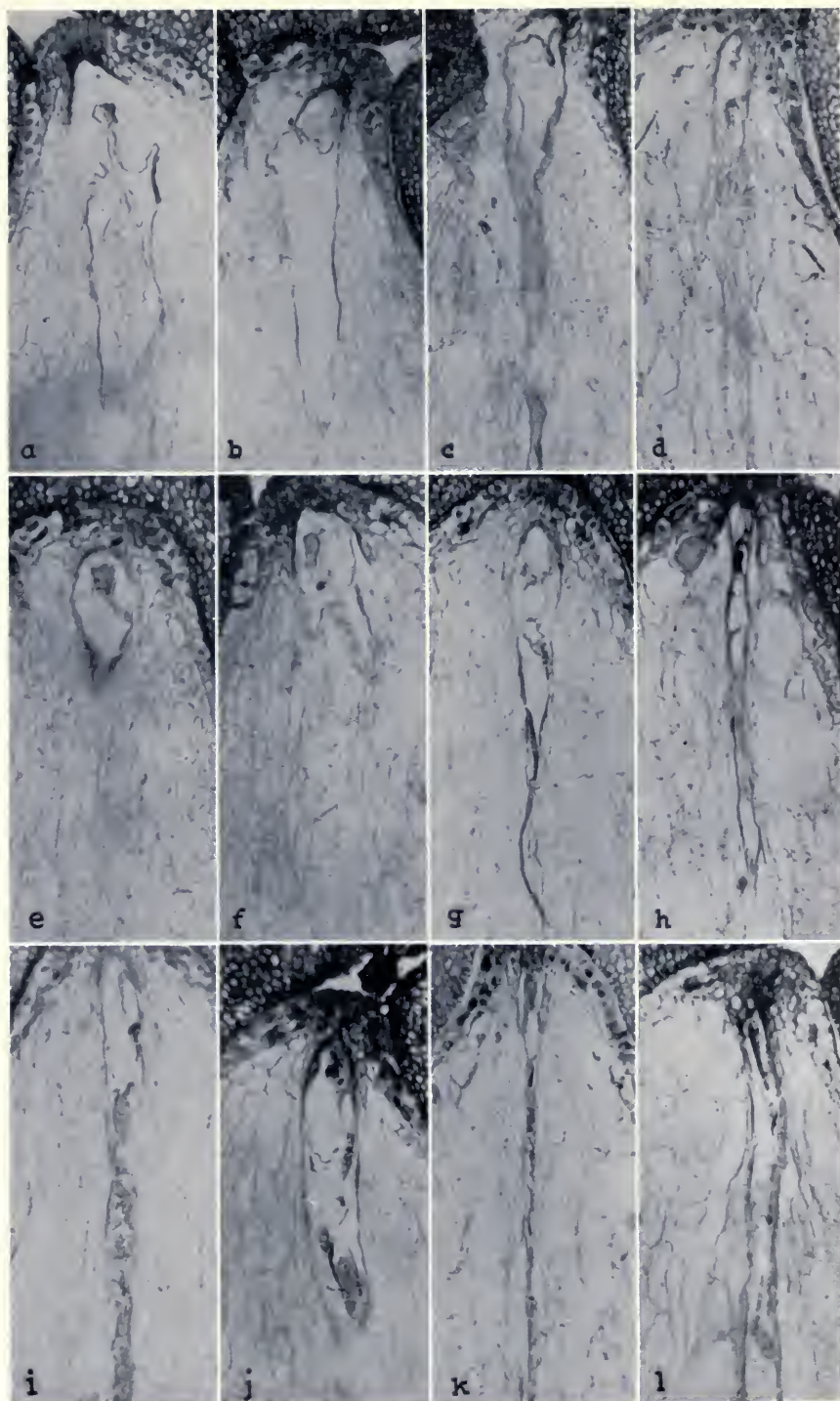


FIG. 3.—RETARDED CONDITION IN EMBRYO SAC OF J. H. HALE BUTTONS
47 DAYS AFTER FULL BLOOM

- a-d*—Advanced stages of disintegration and absorption in contents of embryo sac.
- e-h*—Some of the variables encountered in the condition of the zygote at this stage. Only *g* shows endosperm remnants.
- i-l*—Some endosperm development has taken place but apparently no division of the zygote.

no buttons. The season of 1931 was unusually favorable for growth in the early spring, and because of a crop failure the year before, the trees had "had a rest." Under these conditions the crop of 1931 was not only the heaviest on record in this orchard but in the state as well, and there were very few buttons produced by J. H. Hale during this season.

One collection of pistils was made on April 18, 1931, fifteen days after bloom. From this lot 75 ovules were sectioned for study and compared with those taken in 1929 (Table 1, line 3). Of this number, the embryo sac was aborted in nine. In 3 embryo sacs of the lot there was one nucleus, in 62 there were two, and in 1 there were three. The two-celled condition of the sac was typical of this lot and contrasts with the one-celled condition found in the smaller 1929 sample collected at about the same time after bloom. The general appearance of the sac justified the conclusion that one of these nuclei was the egg^a and the other the fusion nucleus.

The development in the embryo sac in these two lots is interesting in view of the extremes in button production during the seasons of 1929 and 1931. It may be assumed from the 1931 material that the endosperm nucleus did not normally divide in the more vigorous pistils in this variety earlier than two weeks after full bloom. On the other hand, the other nuclei of the embryo sac did not persist much longer than two weeks. It was, of course, impossible to determine from the appearance of the egg and the fusion nucleus whether or not fertilization (i.e., double fertilization) had taken place, and it is very difficult to check the actual time of gametic fusion in any considerable number of pistils. It is probable, however, in view of the results with other fruits, that under the most extreme instances of delay, gametic fusion takes place in the peach within a two-weeks period after full bloom. The absorption of the antipodals and synergids would indicate that in 1931 development in the embryo sac was normal in most instances. Four of the sacs of the 1929 collection, it will be noted, run parallel with the binucleate condition in 1931. Up to this time, then, it does not seem possible to detect any irregularities which can be related to buttons.

Twenty-Three Days After Bloom.—The 188 pistils collected 23 days after bloom in the Bates orchard in 1929 averaged about $\frac{1}{4}$ inch in diameter. The "shuck," or calyx, had been thrown off in most cases.

^aFor convenience, after the normal time of fertilization has been reached and passed, the cell in the embryo sac in the position of the egg will be called the zygote, even tho it is necessary to assume that fertilization has taken place.

Altho the first drop was over when this collection was made, the non-pollinated fruits were still on the tree; and while there was some difference in size, it was still difficult to separate the fruits undergoing normal development from those which would be cut off at the second drop.

A critical study of these 188 pistils revealed the following conditions (Table 1, line 4). A single cell was present in the position of the egg or zygote in 195 ovules (including 7 double ovules). In some instances this nucleus was broken down and disorganized, and as a result it stained deeply (Fig. 2, *e, g, i, l*). Two nuclei were present in the micropylar end of a sac in only three instances. An embryo, five to eight cells in diameter, had developed in only three sacs; and in each of these, endosperm nuclei were present in varying numbers (Fig. 2, *i*). There was no endosperm to be found in the other sacs—185 in number—but in nearly all of them the fusion nucleus was still present (Fig. 2, *g, i, j*).

The ovule had, of course, undergone many structural changes since the former collection at about the two-week period. The embryo sac had extended further into the "canal," or opening, that had formed in the nucellus. The peculiar crinkled appearance of the sac in so many cases (Figs. 2 and 3) indicated something of its lack of normal growth or elongation in the absence of endosperm formation. In these same ovules the canal had increased in length and depth independently of embryo-sac extension. It would seem that a state of development had been reached at the time of this collection when it was increasingly necessary for the pistil structures to complete their normal growth if the fruit was to persist and grow.

In order to evaluate the situation just described, in relation to button production, comparison will be made with normal development in Elberta in which buttons seldom, if ever, occur (Table 1, line 5). In 15 normal pistils of Elberta collected 20 days after bloom in 1933, from the Olney farm, the zygote had divided in only two. Endosperm nuclei were present in varying numbers in all of the sacs except one, in which the fusion nucleus had not yet divided. This pistil was probably the most retarded of the lot because in it the embryo sac had extended into the canal only about one-fourth of the length of the nucellus. In the others the embryo sac was about one-half extended in 4, two-thirds extended in 5, and fully extended in the 5 remaining pistils of this lot.

At the three-week period, while it was still impossible to determine which pistils would form buttons, it was of considerable interest to note the retarded development in such a large proportion of the

ovules of J. H. Hale in a "button year." The absence of endosperm nuclei in so many pistils is especially significant in view of the fact that the time had arrived when there were endosperm nuclei in what appeared to be normal pistils of both J. H. Hale and Elberta. The presence of an embryo and endosperm nuclei in three of the ovules in the 23-day collection of 1929 may be taken as normal development in J. H. Hale at this period for the most advanced pistils. It should be noted that Harrold^{13*} found the zygote nucleus divided in the variety Carman, growing under Georgia conditions, as early as 12 days after fertilization.

Emphasis should be placed on the fact that division in the endosperm nucleus precedes division in the zygote by a week or so. This raises a very important point in connection with button formation: viz., will the zygote nucleus divide if the endosperm nucleus does not? This point will be stressed in the discussion when the condition in the embryo sac in the later collections has been described.

Before passing on to a discussion of the next collection, special mention should be made (*a*) of the persistence of two nuclei—presumably the egg and the fusion nucleus—in such a large proportion of the J. H. Hale pistils, (*b*) the retarded development in the endosperm as compared with Elberta; and (*c*) the absence of pistils with a single nucleus in the sac such as was found in the 16-day collection.

Thirty-Five Days After Bloom.—The next collection was made on May 8, 1929, or a little more than a month after bloom. At this time there was still more difference in the size of the young fruits than at the 23-day period. The second drop was under way, but it was not extensive; so as late as this it was still impossible to select buttons with certainty. There had been considerable enlargement in the ovule since the previous collection. The central cells of the nucellus adjacent to the funiculus were brownish in color and somewhat broken down in many, but not in all, of the ovules examined, indicating further disturbance in that region in some instances. At this stage the embryo sac showed the peculiar crinkled appearance already noted, but in an increasing degree.

Observation of the sections showed many variables in the contents of the embryo sac (Table 1, line 6). In one sac both the zygote and the fusion nucleus appeared normal even tho they had not divided. In 6 others both were greatly distended and showed advanced stages of degeneration. It was interesting to find that as the zygote became distended, the nucleus was basal (i.e., away from the micropyle) to a single large vacuole. In 7 sacs a zygote was present in various stages

of distension and disintegration but in none of these could the fusion nucleus be found. It is probable that in these sacs this nucleus had been absorbed after its disintegration, since it is not likely that a pistil would persist for so long if growth in it was not sufficiently vigorous for embryo-sac development to be carried that far. In one instance, in a double seed, the sac was empty and in two the zygote was absent, altho in one sac there were a few endosperm nuclei. In 6 pistils a normal-appearing embryo a few cells across had developed, and the endosperm nuclei were in active division. These were apparently the normal pistils of this lot of 22 selected at random.

The expansion of the membrane of the zygote in the retarded pistils, where it still persisted as such, and the diffused staining of the cytoplasm indicated that the approximate limit of the functional period had been reached. In fact, the sac itself was often folded and crinkled, a very interesting internal condition in young fruits that have persisted up to the time limits of the second drop.

Forty Days After Bloom.—The next collection in 1929 was made on May 14, about 40 days after full bloom. The difference between the size of the normal fruits and those falling behind in growth was about as follows: The largest of the normal peaches were $\frac{3}{4}$ inch thru the suture diameter, while the retarded fruits averaged about $\frac{7}{16}$ inch in diameter—about the upper limit of the size reached by nonfertilized pistils. The size of the kernel in these two groups was roughly proportional to the outside dimensions, the length in the larger fruits averaging about $\frac{5}{8}$ inch and in the smaller ones nearly $\frac{1}{4}$ inch. With this difference in size between the two groups still persisting, and with the June drop under way, it would seem safe to assume that a part of the fruits in this collection would develop no further than buttons.

From this collection sections were made of 93 ovules. Of this number, a zygote was present in 65. No trace of either a zygote or an embryo could be found in 21 ovules, yet these came from the normal-appearing smaller peaches. Endosperm nuclei were present in 24 sacs, but in 62 none could be found. In most of the latter the fusion nucleus still persisted but was badly disorganized or distended. Both an embryo and endosperm nuclei were found in only 7 embryo sacs in this collection (Table 1, line 7). The canal had extended the full length of the nucellus in all of the ovules, but the embryo-sac extension was quite variable, being fully formed in only a few instances. Even with this internal condition the outer seed coats were whitish in color and the ovule was still plump.

It will now be of interest to compare again the development in normal ovules of Elberta and J. H. Hale. These comparative studies show that embryo and endosperm growth in Elberta (from the 1933 collections at the Olney farm) and normal-appearing, larger fruit of J. H. Hale progress thru the season at about the same rate. This would be expected, since these two varieties ripen so nearly at the same time. The condition in the larger pistils of either of these two varieties might, therefore, be taken as the normal status for the particular stage of development in question.

In sections of Elberta pistils at the 40-day period an embryo six to eight cells across was always present (Table 1, line 8). It has been pointed out (Dorsey and McMunn^{8*}) that as late as two months after bloom the embryo in Elberta is still small, generally no more than $\frac{1}{16}$ to $\frac{1}{8}$ inch in diameter. In contrast to the retarded growth in the embryo, division proceeds rapidly in the endosperm nuclei, so that at the 40-day period the embryo sac is fully extended into the canal and is lined by endosperm nuclei thruout its length. At the 40-day period, development in the embryo and endosperm in buttons on the J. H. Hale was far behind that in normal peaches of either J. H. Hale or Elberta.

Ovule Developments After the June Drop

Forty-Seven Days After Bloom.—The next collection in the 1929 series was made on May 20, which was 47 days after full bloom. The June drop was over; so in this instance for the first time buttons could be definitely selected because of the contrast in size between them and the normal peaches.

After the drops were over, there still remained on the tree two groups of peaches differing greatly in size. The buttons which persist until harvest must, therefore, be derived from this retarded group. After the June drop, however, there is still a slight loss of buttons thruout the summer, especially if buttons make up a large proportion of the crop. This loss always comes from the smaller sizes, which wither and assume a yellowish cast before falling (Fig. 4). This would indicate some competition, or at least some difference, between the buttons themselves; it was shown by the writer (Dorsey^{9*}) that normal peaches are physiologically dominant over buttons.

In view of the persistence of the contents of the embryo sac in the previous collections even tho the zygote showed advanced stages of disintegration, it will now be of interest to note the condition in buttons at the 47-day period (Table 1, line 9).

In the ovules sectioned for examination there was not a single



FIG. 4.—SIZE RANGE IN FRUIT OF J. H. HALE AT END OF JUNE DROP
Note withered condition of the smaller buttons. (*Natural size.*)

instance in which there was a normal development for this growth stage in either the embryo or the endosperm (Fig. 2). The variation found in these structures was interesting. Of the 30 ovules sectioned for study, the zygote nucleus was still recognizable in 24 but had apparently been absorbed, if it had been formed, in 6. The endosperm nucleus had divided and a few nuclei were present in 4 ovules; but it could be recognized, altho in various stages of disintegration, in 13 of the others. In the 13 remaining ovules of this lot the zygote was present but the endosperm nucleus had been absorbed, leaving only a single nucleus in the embryo sac. An interesting feature of this lot was the absence of a simultaneous development of the embryo and the endosperm, and the relatively large number of ovules (19 out of 30) in which either one or the other could not be found.

Thus the condition in the buttons closely parallels that found in the earlier collections, when it could not be stated definitely which fruits would develop into this type. The remnants of the zygote, embryo, fusion nucleus, and endosperm found in the buttons fit into the series terminating with the previous observations. All these structures, when present in buttons, were undergoing disintegration, and the most advanced development found in any of the buttons was far behind that of the normal peaches.

Final Stages.—With the picture of suppressed or retarded growth in the embryo and endosperm in mind, as outlined above, there now remains to be noted the final disposition of the seed and its contents in the buttons. The examination has thus far included pistils collected at intervals extending from bloom, thru the period of the three drops, on to the time when buttons could be singled out with certainty from the normal peaches. The 1929 collections did not extend beyond the 47-day period after bloom, for it was thought that the contents of the embryo sac would probably not persist beyond that time. When it was found, however, that this was not the case, it seemed advisable to make still later collections in order to follow the ovule parts thru the final stage of suppression, disintegration, and even absorption.

The next collection was therefore made 80 days after full bloom (Table 1, line 10). These buttons were divided into two groups, large and small, and these two groups were further divided according to number of ovules which had developed and the coloring of the seed coats.

While the number of ovules in the different categories is not large, nevertheless this series, collected in 1937, shows about the same development in the embryo and endosperm as the buttons showed in the

earlier collections. The persistence of a single cell in the sac in the position of the zygote and the absence of an endosperm nucleus is an interesting feature of these ovules, because it shows that after a certain stage the endosperm nucleus tends to be absorbed much the same as the endosperm. At this late stage too a considerable number of ovules were devoid of a zygote. As with the other collections made at an earlier stage, the endosperm had developed to varying degrees but embryos were present in only a few cases. This series then shows an internal condition which may be looked upon as simply a persistence or a continuation of the earlier condition in buttons found in other years.

A word should be added as to the final stages in the suppression of the seeds in buttons. Soon after the seed coats turn brown, near the end of the second growth period or during the early part of the third, the liquid content of the seed is withdrawn and in a short time the nucellus collapses. All that remains of the kernel at the end of the growing season, then, is the brown, empty, compressed seed coats. Sometimes the seed coats are broken loose from the placenta, in which case there is often a slight exudation of gum in the stone cavity.

This, then, is the course of events in the ovule and seed of buttons. The suppression of the ovule and the endosperm is typical of the final stages. The persistence of the remnants of these structures for so long is not surprising in view of the retarded activity in the growth of the button as a whole. In spite of the internal condition, however, fruits of this type persist and even undergo a remarkable enlargement in the final swell.

PRESENCE OF DOUBLE SEEDS IN BUTTONS

Still another characteristic of buttons deserves consideration—the partial development of both ovules. While in the peach two ovules normally start to develop, one is suppressed in most instances. This condition is also typical of the plum (Dorsey*), in which the time of suppression was found to vary considerably in different species. This point was given some attention in the peach by Harrold,^{13*} who found that in the variety Carman the suppression of one ovule took place normally before bloom or at least before fertilization. Under normal conditions two seeds sometimes develop in some of the other commercial varieties. Thus in two varietal combinations in the greenhouse crosses the following condition was found in 1933: among 224 normal peaches of J. H. Hale X Gage there were three that had "double seeds," and in 169 fruits of Gage X Elberta¹ picked at maturity there were three that were "doubles." The seed condition in

buttons, however, is quite different from that in normal peaches, as will be seen from Table 3.

While the data in Table 3 show that there is some variation from year to year in the proportion of double seeds in buttons of J. H. Hale, the number is much larger than in normal peaches. The development of both ovules to the extent found in buttons, however, is evidently not a deciding factor in button production, for buttons are also found with a single ovule partially developed. Double ovules may, therefore, be taken as an index of the extent to which there is a parallel development in the two ovules in this variety before fertilization becomes a deciding factor in the early stages of growth. The size of the seed-coat remnant of the suppressed ovule in normal peaches is comparable

TABLE 3.—CLASSIFICATION OF BUTTONS, AFTER THE JUNE DROP, WITH REFERENCE TO SINGLE OR DOUBLE SEED CONDITION, J. H. HALE

Year collected	Location	Number with one seed	Number with two seeds	Total
1927.....	Centralia	27	26	53
1927.....	Alto Pass	83	38	121
1928.....	Centralia	149	144	293
1929.....	Centralia	233	36	269
1937.....	Centralia	487	110	597
1938.....	Flora	174	71	245
Total.....	1 153	425	1 578

to that in buttons. This indicates that in the absence of fertilization suppression in the second ovule takes place at about the same stage in both buttons and normal peaches. In buttons, therefore, something has happened to the second ovule which does not ordinarily happen in the normal peach. Since the two ovules in buttons are so nearly the same size even tho partly suppressed, it would seem logical to assume that similar development has taken place in both of them.

During midsummer considerable variation is always apparent in the size of buttons. It therefore seemed advisable to determine whether or not this difference was related to the double-seeded condition. The data collected on this point during three seasons have been brought together in Table 4.

The collections recorded in Table 4 were made, it will be noted, at about the same time after bloom. Each lot was divided into three size-groups and one wilted lot to include the buttons that were being eliminated by late summer abscission. These categories were further divided according to the seed number and the seed-coat color, but

no significant relationship could be observed between the partial development of both ovules and either size or the time of browning of the seed coats. The collections were made early enough in 1929 and 1937 to include a considerable proportion of wilted buttons, which would have been eliminated by abscission within a few days.

There is one significant feature of the 1938 data which was not encountered in either of the other two seasons—in nearly one-fourth of the buttons the developing ovule had aborted at an early stage. Six

TABLE 4.—SIZE, SEED CONTENT, AND COLOR OF THE SEED COATS OF BUTTONS NEAR END OF SECOND GROWTH PERIOD

Number of seeds developed	Color of seed coats	Number of buttons in the different size-groups on date of collection				Total
		Large	Medium	Small	Wilted	
1929: 84 days after full bloom						
2	Brown.....	25	10	0	1	36
2	White.....	0	0	0	0	0
1	Brown.....	24	82	79	35	220
1	White.....	3	9	1	0	13
	Total.....	52	101	80	36	269
1937: 78 days after full bloom						
2	Brown.....	14	5	0	76	95
2	White.....	10	5	0	0	15
1	Brown.....	33	36	0	387	456
1	White.....	24	7	0	1	32
	Total.....	81	53	0	464	598
1938: 90 days after full bloom						
2	Brown.....	13	0	0	0	13
2	White.....	1	1	0	0	2
1	Brown.....	23	59	16	6	104
1	White.....	15	26	4	0	45
1	Aborted.....	6	16	30	0	52
	Total.....	58	102	50	6	216
Total button production in these three years						
..	191	256	130	506	1 083

of these buttons even fell into the large-size group. The seed-coat remnant in these buttons was larger than that of the suppressed ovule, and from its appearance it seemed that it had ceased enlarging at about the two- or three-week period. Subsequent growth in buttons under these conditions is comparable to that of peaches with frost-killed seeds.

CONTROL MEASURES TESTED

Experiments carried out with the J. H. Hale in 1929 and 1931 to determine whether buttons might be prevented, or at least controlled in part, by cultural methods proved, for the most part, negative. These tests were started before the more detailed studies of the condition in the embryo sac were under way and included pruning, nitrate applications, and pollination. The experiments were limited to these three treatments because any one or all of them could be readily used in the regular cultural program.

Pruning.—The pruning variables set up included a light thinning out of 14-year-old trees at one extreme and a heavy pruning, almost dehorning, at the other. The trees thus treated (Bates orchard) bore a crop in 1929. While the production of buttons on the vigorous growth resulting from the heavy pruning was lighter than in the other type of cutting, the pruning measures did not prevent or appreciably reduce the formation of buttons. This point was tested, it will be noted, during a heavy button year.

There was also an opportunity in 1929 to check vigor of growth in relation to button production under a wide range of conditions in the state, and no definite relationship with shoot length or vigor of growth was apparent.

Nitrate Applications.—The question arose a number of times as to the possibility of avoiding the production of buttons, at least in part, by increasing the available nitrogen supply during the prebloom period. A fertilizer test was run in the Bates orchard in 1931 to check this point.

An isolated block with suitable pollinizers some distance away, but with "bouquets" placed in the trees at rather frequent intervals, was divided into plots. On March 6 the following treatment was applied: 20 trees were given 2½ pounds of nitrate of soda each; 10 trees, 5 pounds each; 40 trees, 10 pounds each; and 10 trees, 15 pounds each. The season of 1931 was not a big "button year" in this orchard, but buttons were present in considerable quantities.

On July 11, after the June drop was over, there were no differences to be seen in the set or in the production of buttons in these different plots. The foliage of the trees receiving the heavier application was, however, deeper in color and the terminal growth was longer. Since the production of buttons was relatively light, the crop was heavy in 1931—so heavy, in fact, that the trees had to be thinned. This test was made in the same part of the Bates orchard which produced a heavy button crop in 1929.

Pollination Experiments.—When this study was started, it seemed advisable to determine what bearing, if any, the source of the pollen might have upon the production of buttons. The first crosses made with this objective in view were made in 1929 in the Bates orchard on J. H. Hale trees which had been heavily pruned the previous year and also on old slower-growing trees. The records of these crosses on the heavily pruned trees and some subsequent crosses as well are given in Table 5.

TABLE 5.—BUTTON PRODUCTION IN CONTROLLED CROSSES

Cross	Number of flowers pollinated	Number of fruits harvested	Number of buttons
<i>1929</i>			
J. H. Hale × Perfection Cling.....	410	169	7
J. H. Hale × Gage.....	788	204	7
J. H. Hale × Gage.....	1 380	50	1
J. H. Hale × Elberta.....	734	169	6
J. H. Hale × Elberta.....	1 289	91	2
J. H. Hale × Late Elberta.....	538	145	2
J. H. Hale × open-pollinated.....	1 500	9	11
<i>1933</i>			
J. H. Hale × Gage (greenhouse).....	78	10	0
J. H. Hale × Gage (greenhouse).....	106	51	0
J. H. Hale × Gage (greenhouse).....	115	46	0
J. H. Hale × Gage (greenhouse).....	50	35	0
J. H. Hale × Gage (greenhouse).....	273	34	0
J. H. Hale × Gage (greenhouse).....	407	72	0
<i>1937</i>			
Halehaven × unknown.....	Whole tree	73	21
Unknown × Halehaven.....	4-yr.-old tree	28	20

Three things are of importance in this connection in Table 5.

First, buttons were produced by J. H. Hale in 1929 when pollinated by three different varieties. Buttons were also produced when flowers were emasculated but open-pollinated. Since it seemed at this time that pollination might be an important factor in button production, bee activity was studied in the Bates orchard on trees adjacent to a row of Perfection cling. Hives of bees were placed at frequent intervals along the row. Thus located, the bees had ready access to Perfection cling, which produced pollen in abundance. They worked actively on this variety under very favorable flying conditions, but they worked very little on the J. H. Hale trees adjacent to the hives. They seemed to distinguish readily between the two, since pollen was available from one but not the other.

Second, buttons were produced in relatively large numbers in the two crosses in which Halehaven was included. This suggests the possibility of a hereditary factor having some bearing upon button production.

Third, it is especially significant that buttons were not produced on any one of the six trees used in the greenhouse crosses pollinated with Gage pollen.

GENERAL DISCUSSION OF THE PROBLEM

Necessary Steps in Early Fruit Development

The growth and enlargement of a peach must be viewed as a series of growth processes which in reality extend from fruit-bud initiation one season to harvest the next. Looked at in this way, the ripe fruit is the end-result of development in those pistils in which all of the necessary steps have taken place normally in that part of the cycle between bloom and maturity. Three growth periods are now generally recognized in this part of the cycle. If a peach is to complete all three of these, it must pass thru three critical stages in the first period:

1. Complete development in the peach flower at full bloom may be taken as the first critical stage. From the standpoint of fruit setting, this includes a perfectly formed stigma, receptiveness, and an embryo sac with typically the full nuclear content of eight. If for any reason growth is suppressed short of this, fertilization probably cannot take place and the pistils or flowers are cut off at the first drop, thus definitely eliminating them from that group which later form buttons.

2. If pistil development is normal up to full bloom and all of the nuclei in the sac are functioning, the next necessary step in the continuance of growth is pollination and fertilization. A number of self-pollination tests with the J. H. Hale variety at this Station verify the results of Connors^{3*} in New Jersey in showing that nonpollinated, and hence nonfertilized, fruits drop. The most vigorous pistils, however, were found to persist for 35 days or so and to lengthen as much as $\frac{3}{8}$ inch. It may be concluded from these experiments that buttons do not come from nonpollinated or unfertilized pistils.

3. The next critical stage to be reckoned with is fertilization. As ordinarily understood in the higher plants, this means double fertilization, as a result of which growth is initiated and made possible in both the embryo and the endosperm. While, in the peach, fertilization does not necessarily insure complete development in the fruit, for there is generally a June drop composed of pistils in which there may be both an embryo and endosperm (Detjen^{5, 6*}), nevertheless fertilization—that is, double fertilization—is essential for the

completion of the entire growth cycle in the peach fruit. This being the case, it would seem that something has happened in buttons which falls short of the normal process of double fertilization but which enables the fruit to persist even tho it does not reach full size.

Growth Stimulus to Fruit From Fertilization

With the ground thus limited for a discussion of some of the possible causes of buttons, it will be interesting, first, to consider briefly the growth stimulus to the fruit as a whole which comes from fertilization. While there is always some variation to be found in the time the different flowers on a tree open or in their relative size and advancement immediately afterward, a pronounced difference between them comes soon after fertilization. The stimulus from this process, whatever its nature, sets up a differential in the rate of growth so that it is possible soon afterward to select those peaches which may be expected to undergo normal development. The time at or during which this stimulus affects growth is a matter of considerable interest. Fortunately observations made on three occasions—two in the progress of this study—throw some light upon how early growth may be suppressed in the ovule or seed and still have enlargement continue in the stone and flesh.

The first incident to be noted occurred in the spring of 1927. On April 22, and in some places on April 23, the temperature fell as low as 26° F. and 27° F. in southern Illinois and northern Kentucky. The period of bloom of the peach in this area ranged from March 7 to 10 in the Ohio river area between the two states, to March 20 and April 1 farther north in Johnson and Union counties in Illinois. In the J. S. Whitmire orchard near Rosebud, in Pope county, the peaches were about $\frac{1}{2}$ inch in length when the freeze came. This was 30 to 35 days after full bloom. The ovule at the time was generally slightly less than $\frac{1}{4}$ inch in length. The approximate stage of development in the embryo and endosperm can be seen by referring to the discussion of Elberta at the 40-day period from bloom (page 19). On account of the variation in development, as expressed in the time of bloom from south to north, the seeds were killed at different sizes, varying from $\frac{1}{4}$ inch in Union county to $\frac{3}{8}$ inch in Kentucky. The largest peaches of Elberta toward the southern border of the frost zone in Kentucky were at the time of the freeze about an inch in length.

This situation was studied rather widely in southern Illinois, and the percentage of Elberta peaches with dead seeds after the June drop was found to vary in different orchards from 15 percent to 30 percent

of the crop. Some observations were made also on J. H. Hale, but the studies were confined, for the most part, to Elberta. There was much uncertainty as to just what would happen to those fruits with the dead seeds, so arrangements were made to study the situation from time to time until maturity.

As the season advanced, most of the peaches with the dead seeds were found to persist (Fig. 5). The stone in these peaches reached nearly full size but hardened a few days later than in the normal peaches. Because the kernel was suppressed, the seed cavity was very much compressed (Fig. 6), and by midseason in many of the stones



FIG. 5.—PEACHES WITH NORMAL SEED AND WITH DEAD SEED

The bottom row shows J. H. Hale peaches in which the seeds were killed 30 to 35 days after bloom. In the top row are normal peaches. (*Natural size.*)

with dead seeds there were varying amounts of gum. Sometimes the stone was "split" in these peaches, but generally it was not.

The relation between the growth of the fruit and the presence of dead seed is shown by a random sample of 151 peaches collected on June 27 (more than 100 days after bloom) in the Whitmire orchard. These were first divided into two lots according to their size. They

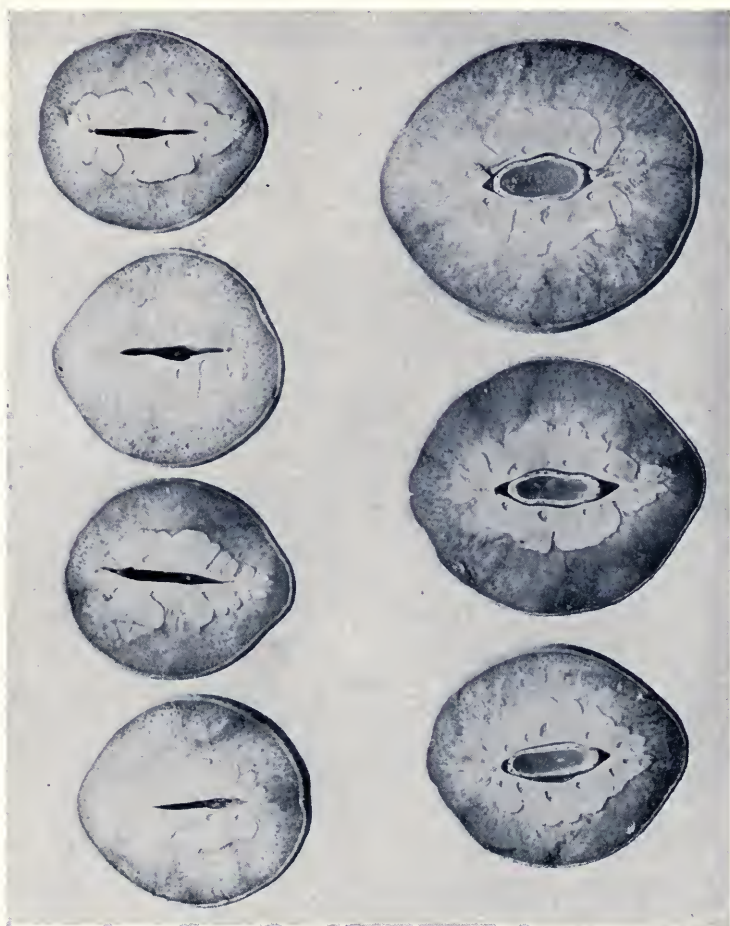


FIG. 6.—SEED CAVITY OF KILLED SEED AND NORMAL STONES

At the left are Elberta peaches after the stone-hardening stage, showing the compressed seed cavity when the seed is killed. The fruits at the right show the normal stone development that takes place when the seed is not killed. (Natural size.)

were then cut open and the seed condition noted. In the group of larger fruits 53 peaches had normal seeds and 53 had dead seeds. In the group of smaller fruits 6 bore normal seeds and in 39 the seeds were killed. The dead seeds were completely dried up but the collapsed seed coats could always be found. This general situation prevailed at harvest, altho the peaches with the dead seeds tended to ripen a few days before the others. Some of the largest fruit, however, belonged to the dead-seed group.

The next instance to be noted was the subsequent development of the buttons with aborted seeds in the 1938 collection (Table 4). The seed-coat remnant in these buttons was only $\frac{1}{8}$ inch or so in length, tho this is considerably larger than the usual remnant of the suppressed ovule. In these buttons the seed seemed to have been killed at an early date—probably soon after the time of fertilization—yet the growth stimulus from fertilization had taken place. In any event, the buttons with this seed condition persisted and enlarged much the same as the others. The date of the suppression of the ovule in this instance could not be determined definitely; so the size of the seed coat is the best index of the stage reached.

In addition to these two instances, the observations of W. W. McGill, extension horticulturist at the University of Kentucky, will be of interest. He reports that in the spring of 1938 peaches were in bloom in northern Kentucky about March 23 to 26. A frost came April 11, during which the temperature fell as low as 28° to 30° F. As in the Whitmire orchard instance just cited, the seed was killed in varying percentages of the crop in different orchards in the frost area. In midsummer a large proportion of the peaches with the killed seeds were making an apparently normal growth. This instance places the killing period only 16 days or so after bloom^a and very near the time of the division in the zygote nucleus, which, of course, would be after division in the fusion nucleus.

The above observations are interesting in view of the experiments of Tukey^{26*} in killing the embryo in growing peaches. He found that when the embryo was killed by boring thru the flesh and stone into it with a small drill as early as the second growth period, there was an "abrupt check in fruit development, shriveling, and abscission." On the other hand, when the embryo was killed in the transitional stage between the second and the third period, the growth rate of

^aSince the above was written, Havis^{14*} has reported the results of a freeze in Ohio, about three weeks after bloom, in which the peaches persisted after the seed was killed.

the fruit remained about the same for a limited period "but ended with earlier ripening and a failure to reach full size." When still later in the third period the embryo was killed, there was an increase in the growth rate in the flesh but earlier ripening.

While Tukey's experiments are suggestive in showing something of the relationship between growth in the seed and the flesh, they do not throw much light upon the problem at hand because the stage of development in the seed parts was far beyond that reached in buttons.

The evidence from the early killing of the ovule and the seed is important in an analysis of the disturbance which terminates in buttons. The fact that both buttons and peaches persist and enlarge after the seed has been killed at an early stage shows that the stimulus to growth comes at an early date, and that when it once occurs its influence upon the structure as a whole extends on to maturity. In the evidence from this angle two items are especially significant. First, in the earliest killing observed in Elberta the ovule had enlarged to about the size reached in buttons, yet growth proceeded in the fruit far beyond the size reached by buttons. Second, the growth rate in buttons is not materially affected by the ovule being eliminated by being killed at an early date. It would seem, in the light of subsequent events, that there was some essential difference between the buttons and the peaches before the seeds were killed. The mere persistence in buttons of either a single or a double ovule after the approximate time of fertilization, tho interesting, is apparently of little consequence in influencing growth.

Departures From Normal Seed Development

Consideration should now be given to some of the variations encountered in the sexual process in plants, in order to evaluate their counter bearing upon the production of buttons in the peach.

The first variation to be reckoned with is parthenogenesis (reduced or unreduced). This factor can be definitely eliminated from consideration, however, because when unpollinated peach pistils are left to develop, as noted above, they persist for only about 40 to 50 days at most. Likewise, the production of supernumerary embryos, as in citrus (Swingle^{24*}), where there is a budding or growth of the nucellar cells into the embryo sac, which gives rise to embryos which are identical genetically with the seed parent, can be eliminated from consideration. In "seedless fruits" also there are varying types of development in the ovule and carpel parts, resulting in some instances in an edible fruit being formed without seed development. In some of

these cases pollination seems to be necessary to initiate growth, but the extent to which pollen-tube growth only stimulates development has not been ascertained.

Stimulating agents have been used to induce development in fruits in varying degrees. Recently Gustafson^{11*} has shown that in some plants the pollen produces a chloroform-soluble substance which initiates growth in the ovary and sometimes causes seedless fruits to develop. In the experiments of Gardner and Marth^{10*} abscission was prevented in the holly and development comparable to that in pollinated flowers was stimulated in the pistil parts by spraying them with "growth promoting" substances. Experiments of this kind are interesting from the horticultural standpoint because crop production is normally based upon the persistence of fruits after both pollination and fertilization. At the same time, use has been made of some plant forms which develop edible fruits from a more-or-less vegetative growth in the receptacle or ovary wall in the absence not only of fertilization but in some cases pollination as well.

It would thus appear that the type of development found in buttons does not fall within any of the above classes.

There is, however, in the work of Nixon^{17, 18*} and Swingle^{25*} an analysis of the pollen-embryo-endosperm relationship to fruit development in the date, which is suggestive in this connection. Their results show that pollen from different varieties has an influence upon size of fruit, shape of seed, and also time of ripening. Since the effect of the pollen upon fruit development is supposed to be thru the growth and formation of the embryo and the endosperm, the term "metaxenia" was proposed by Swingle in 1926 for the influence these structures exert outside the embryo sac.

Swingle^{23*} says, in speaking of the effect of different pollens upon fruit development in the date, that the simplest hypothesis is that the embryo or the endosperm or both together "constitute a ductless gland apparatus that affects, by secreting hormones, the development of the whole date fruit including tissues belonging morphologically to the mother plant and especially to the thickened ovary walls which constitute the edible portion of the date fruit." A similar influence is believed also to come from supernumerary embryos in citrus fruits. It should be noted that Swingle considers that the stimulus may come from either the embryo or the endosperm or both. This situation is somewhat different, therefore, from that found in buttons of the peach, for in buttons neither of these structures develops normally.

This same phenomenon has been studied by Nebel^{16*} in the apple.

By using the statistical method of analysis, he found slight dissimilarities in fruit resulting when one variety was pollinated with certain others.

In the date and the apple, it should be noted, the differences in the structure as a whole came when both embryo and endosperm were functioning normally, these two fruits differing in this respect from buttons, in which neither embryo nor endosperm is normal.

Conditions in Embryo Sac of Buttons

Before commenting upon the condition found in the embryo sac of buttons, it seems desirable to restate the following points which seem basic to an analysis of the situation: (*a*) unfertilized pistils abscise for the most part at the first and second drops (this category would include, in all probability, those pistils in which there was pollen-tube growth up to entrance of the tube into the embryo sac if gametic fusion did not take place); (*b*) since normal peaches generally bear fully developed seeds, i.e., seeds in which both the embryo and the endosperm complete their growth cycle, it would appear that double fertilization was necessary to initiate this development; (*c*) the evidence from killed seeds in both buttons and peaches shows that a growth stimulus to the fruiting structure as a whole takes place at the time of fertilization, or soon afterward, and that once this stimulus is given, the presence of a normal seed from that time onward is unnecessary for growth in the stone and flesh; (*d*) it is assumed in the following discussion that gametic fusion is necessary to initiate division in both the zygote and the endosperm nucleus.

We may now turn to a brief summary of the condition found in the embryo sac of buttons, as revealed in the more than 600 ovules (Table 1) sectioned for critical examination. Within three weeks or so after bloom, the number of nuclei in the embryo sac were found, for the most part, to be reduced to two—probably the zygote and the endosperm nucleus. Then, taking the condition in Elberta as typical, it was found that the time of active division in the endosperm nuclei started about 18 to 20 days after bloom. This is about a week or so ahead of division in the zygote and constitutes the initial step in endosperm formation.

In buttons, however, the division in the zygote was found to be greatly retarded. In 370 of the 600 ovules reported in Table 1, the endosperm nucleus did not divide. If gametic fusion is necessary to initiate division in this nucleus, the interpretation is that in this group fertilization was limited to the egg. The 98 ovules in which the

fusion nucleus was absorbed probably belong to this same group. This leaves only 79 ovules in the later collections in which varying quantities of endosperm nuclei or cells were present. In these, on the above basis, it would appear that gametic union had taken place with the fusion nucleus but not with the egg, otherwise they would have developed into normal peaches. This interpretation, of course, makes it necessary to assume that the fertilization of either the egg or fusion nucleus is equally effective and comparable in inducing growth in buttons. The validity of this interpretation can now be followed in the other types of development found in the embryo sac.

With the above condition in the fusion nucleus in mind, it is significant to find that in a total of 480 ovules (Table 1) the zygote did not divide. Since this number corresponds so closely to the 468 ovules in which the endosperm nucleus did not divide or in which it was absorbed, it would seem that division in the zygote is dependent upon division in the endosperm nucleus. This is an especially important point in interpreting the condition found because (*a*) division in the endosperm nucleus normally precedes that in the zygote, and (*b*) unfertilized pistils drop. A zygote could not be found in 28 ovules in the late collections, so it is probable that in these it had either been absorbed or lost in sectioning and staining the material. An embryo was found in only 18 ovules—16 of which were in the early collections before buttons could be selected with certainty. In the two remaining ovules there was no endosperm present at the 80-day period. An early degeneration or absorption of the endosperm in these ovules after the initial divisions seems probable.

It would seem then, in the light of the above analysis, that single fertilization, i.e., fertilization of *either* the egg or the fusion nucleus, is the most probable explanation of buttons. Thus, limited in the normal growth stimulus that comes from double fertilization, the fruit persists but enlarges only partially. The interdependence of the embryo and the endosperm is shown, first, by the failure of the zygote to divide when division in the endosperm nucleus does not occur; second, by the failure of the embryo (which normally remains very small until well into the second growth period) to enlarge without endosperm development; and finally, endosperm growth does not appear to proceed far when the egg is not fertilized.

Most Probable Cause of Buttons

Since button production seems to be so definitely related to periods of low temperature following bloom, considerable interest now centers

around some of the possible departures from the normal procedure in double fertilization which may be affected by retarded growth or delay. There may be irregularities in the production of gametes, since pollen transfer is light at best when there is unfavorable weather for pollination. Pollen-tube growth would be retarded by low temperatures, which alone could result in delayed fertilization. If division in the generative nucleus was prevented or made irregular, so that one of the gametes could not function, there would, of course, be in each tube only one nucleus with gametic potentialities. A possible situation could also arise in delayed fertilization in which the fusion nucleus would be involved in the absorptive process, like the antipodals and synergids, to such an extent that union with the second male gamete could not take place. At low temperature levels all of the processes of fertilization may be so delayed that a considerable period may elapse between the time the egg and fusion nucleus are fertilized. This may set up irregularities in development, since there appears to be such a high degree of interdependence between the zygote (or embryo) and the endosperm. The relatively high proportion of sacs in the 1929 collection (Table 1, line 2) with only one nucleus in the sac would be suggestive if there were not such a preponderance of sacs with two nuclei later on, indicating the disposal of the one-nucleus sacs in the first two drops.

There are still other possibilities to reckon with. Single fertilization could take place in both ovules. This possibility is reflected in the nearly equal development in the two ovules in the double seeds which occur in such a high proportion of buttons. In this case, the egg may be fertilized in both ovules, the fusion nucleus in both, or the egg in one and the fusion nucleus in the other. In any event, a "double dose" of the growth stimulus from the two ovules does not seem to increase the size of the button. Fertilization may also be affected by prolonged cold weather thru irregularities in the division of the embryo-sac nuclei. Irregularities in chromosome distribution in some of the divisions observed in these nuclei could easily result in lethal combinations. Some of the nuclei could, of course, be killed, as is suggested in some of the instances of extensive button production. This possibility must be noted particularly in the case of the egg or zygote, since the latter failed to divide in such large numbers. It is probable, however, that delay in gametic fusion may be equally serious from the standpoint of suppression, especially in the fusion nucleus, since in unfertilized pistils it tends to be absorbed next after the antipodals and synergids. Then, too, there is the possibility of a

nucleus being restored, if division has been long delayed, when the temperature rises rapidly. Furthermore, nutritional disturbances, especially in the nitrogen supply, may tend to aggravate the seriousness of some of the above factors.

It will be appreciated, of course, that it is difficult to check some of the variables discussed above because buttons cannot be selected with certainty until the second growth period, which starts 45 days or so after bloom. For that reason increased importance is attached to the persistence of the structures in the ovule. In the light of normal development the antecedents of the condition found can be fairly definitely postulated.

While, as is apparent from this analysis, there is difficulty in stating definitely just what happened to the early stages of the 2n generation to produce this result, yet since it is the unfertilized pistils that drop, the facts warrant placing the difficulty at this point in the growth cycle. This discussion has therefore centered around the idea of a growth stimulus coming to buttons from the fertilization phenomenon—single fertilization in this instance. Any condition which would prevent the initial division in the zygote or the endosperm nucleus would influence the growth of the fruit as a whole because complete development in the peach normally includes a seed. The dependence of the zygote upon the endosperm, and vice versa, has therefore been emphasized.

Finally the question may very well be raised as to why button production is so extensive in the J. H. Hale variety. There is no evident answer to this question in the present approach; but this variety has one characteristic that is suggestive of an explanation in light of the possible effect of low-temperature periods upon the processes involved in the set, and that is that it is pollen-sterile, or at least nearly so. At best, this characteristic would result in a light transfer of pollen, for bees do not "work" on this variety if they are after pollen, especially if other varieties are near. Sections of pistils collected at random at full bloom show a surprisingly light pollination when conditions are favorable for bee and other insect flight. Light pollination would tend to reduce the chances of favorable genetic combinations taking place at fertilization, compared with other varieties, especially if division in the generative nucleus was affected by low temperatures.

Under normal conditions there is much variation in the development found in the embryo and endosperm at midseason, as shown in Fig. 7, which illustrates a range from double seeds to a suppressed

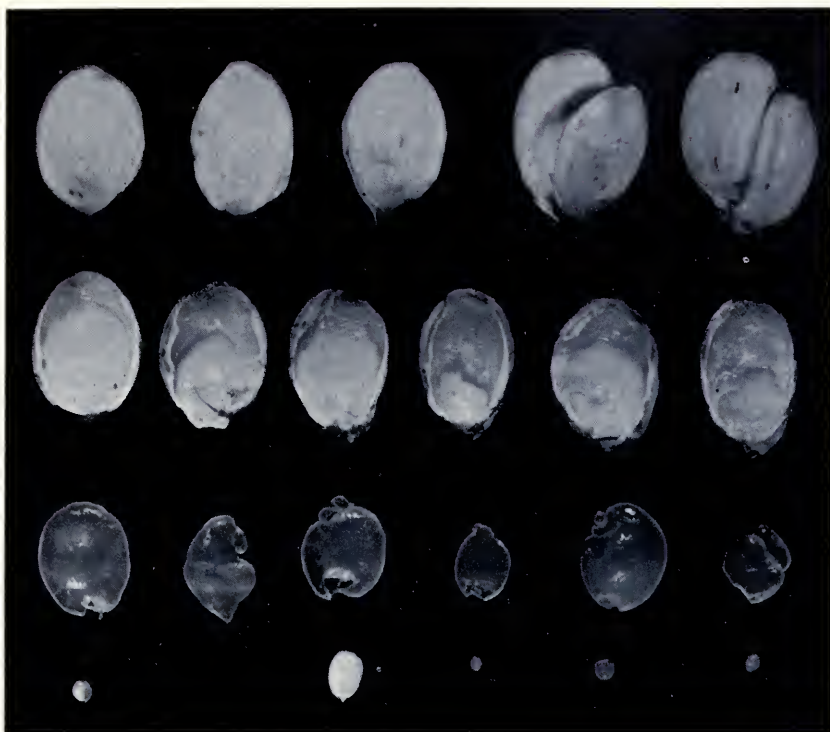


FIG. 7.—VARIATION IN DEVELOPMENT OF SEED IN J. H. HALE PEACHES, 1931

Under normal conditions these seeds would all have been approximately the same size. Note double seeds in the first row, the variation in the endosperm-nucleus relationship in the second, and in the last two rows the endosperm-embryo relationship. (*Natural size.*)

embryo. That there is considerable difference in the extent of growth in both the endosperm and the embryo at a given period is evident in the two lower rows, where the embryo and its respective endosperm are shown separated. A similar variation is shown in the endosperm-nucleus relationship indicated in the second row of seeds. In Fig. 8 is shown the variations found in the size of buttons on seedling trees during the season of 1939.

It will be seen from the general trend of this analysis of the button problem in the peach, that emphasis has been placed upon the bearing which unfavorable weather has on gametic fusion rather than upon injury to the vascular conducting tissue, as has been suggested by Harrold and Blake. The type of disorder found in the chalazal region



FIG. 8.—BUTTONS FROM SEEDLING TREES AT HARVEST TIME
BUT BEFORE FINAL SWELL

Each button is from a different tree and was selected as typical of that particular tree.

of the seed coats would thus be a consequence of suppressed growth rather than its cause. Furthermore, a study of the vascular tissue of buttons did not reveal any abnormalities in the strands leading to the embryo except possibly in size or diameter. However, the final swell in buttons indicates that the vascular bundles leading to the flesh function much the same as in normal peaches.

SUMMARY AND CONCLUSIONS

1. A variable proportion of small retarded peaches called "buttons" is formed in the J. H. Hale variety. Some seasons fruits of this type constitute as much as 90 percent or more of the crop. While this variety produces buttons in greater quantities than other varieties, it is not the only one with this characteristic.

2. Compared with normal peaches, buttons show the following characteristics: (*a*) they survive all three of the drops; (*b*) they fall behind normal peaches in the rate of enlargement during the first growth period; (*c*) the stone is greatly reduced in size and hardens a little later than in normal peaches; (*d*) they ripen later than the other part of the crop and sometimes reach a surprisingly large size.

3. In normal peaches division in the endosperm nucleus occurs about 20 days after full bloom, and in the zygote a week or so later. In buttons, on the other hand, development in the embryo and endosperm is either completely suppressed or, if it occurs at all, it is greatly retarded.

4. In light of the condition found in the embryo sac of buttons at a time when growth had progressed far enough to separate fruits of this type from those which fall at the June drop and from normal peaches, single fertilization seems to be the most probable cause of this condition. The term "single fertilization" is used in this instance to apply to gametic fusion with either the egg or the fusion nucleus.

5. J. H. Hale and a few other varieties are inherently sensitive to adverse weather during the critical growth stages centering around pollination and fertilization. The retardation of the growth processes, or the light pollen transfer when the weather is unfavorable, seems to be an important factor in the production of buttons. For this reason corrective measures are difficult to apply.

6. This study shows three distinct levels (to use the terminology of Sinnott^{21*}), in the growth and development of the fruit of the peach, which can be related to the phenomenon of fertilization: first, the persistence and development of the pistil, in the absence of fertilization, up to a fairly definite limit but no further; second, the retarded growth of the fruit in buttons, which seems to be associated with single fertilization; third, normal fruit growth and enlargement following double fertilization.

7. The fact that the fruit grows after the seed or the ovule is killed by freezing places the initiation of the growth stimulus to the fruit as a whole, which comes from fertilization, at or soon after gametic fusion. Once this stimulus is given to the fruit, its enlargement

continues without the seed, resulting in the different growth levels noted above. This stimulus seems to be fractionated in single fertilization, as contrasted with the stimulus that results from double fertilization.

8. Restricted commercial plantings are recommended for peach varieties showing a tendency to produce buttons with any great degree of regularity.

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